

## A portable whole canopy gas exchange system for several mature field-grown grapevines

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### Summary

Six flow-through chambers (8 m<sup>3</sup> volume) were built to measure gas exchange (CO<sub>2</sub> and H<sub>2</sub>O) of whole vines under deficit irrigation regimes that imposed water stress at different stages of berry development. Chamber design and materials were selected to minimize environmental effects, and to accommodate the trellis of a mature, field-grown vine. A framed design allowed the chambers to withstand sustained winds up to 13 m s<sup>-1</sup>, overcoming one disadvantage of the balloon-type chambers. At mid-canopy height, 1.6 m, air temperature inside the chamber was no more than 2.5 °C higher than at the same height in the canopy of an unchambered vine. Over 24 h, solar radiation inside the chamber was 90 % of ambient. For vines irrigated according to standard industry practice, maximum values of net CO<sub>2</sub> exchange approached 12 μmol m<sup>-2</sup> s<sup>-1</sup>, whereas in water-stressed vines the maxima approached only 6.5 μmol m<sup>-2</sup> s<sup>-1</sup>. Transpiration among water-stressed plants was reduced, with maximum rates at 1 mmol m<sup>-2</sup> s<sup>-1</sup> while vines under standard irrigation were at 2.5 mmol m<sup>-2</sup> s<sup>-1</sup>. Apparent light saturation for canopy photosynthesis was approximately 1200 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD (photosynthetic photon flux density) for vines under standard irrigation, and about 800 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD for vines under water stress.

**Key words:** chamber, open-system, photosynthesis, transpiration, *Vitis vinifera*, irrigation, water stress, whole canopy.

### Introduction

Photosynthesis measurements indicate net primary productivity. Most photosynthesis measurements have been recorded on single leaves and there are several commercial instruments available. However, in large, trellised canopies like grapevines and some fruit trees, single leaf measurements often provide incomplete and somewhat misleading data compared to whole plant net primary productivity (CORELLI-GRAPPADELLI and MAGNANINI 1993, LONG *et al.* 1996, PONI *et al.* 1997). The photosynthetic capacity among leaves in a grapevine canopy differs due to leaf age (KRIEDEMANN *et al.* 1970, SCHULTZ 1993), light exposure (IACONO and SOMMER 1996, ZUFFEREY *et al.* 2000) and position on the shoot (HUNTER

and VISSER 1989, PONI *et al.* 1994), crop load (NAOR *et al.* 1997, PETRIE *et al.* 2000), and leaf prehistory during lamina expansion (GAMON and PEARCY 1989, SILVESTRONI *et al.* 1992, SCHULTZ *et al.* 1996). Scaling-up from single leaf measurements to whole canopy photosynthesis measurements is not straightforward, as the latter is a measurement of leaves of different age and degree of light exposure, as well as other organs like fruit, shoots, and trunks (BUGBEE 1992). Estimation of leaf area distribution and light extinction by the canopy combined with a directional treatment of incident light is needed to estimate whole canopy photosynthesis from single leaf measurements (GIAGLARAS *et al.* 1995, DE PURY and FARQUHAR 1997). Transpiration is reduced by the boundary layer of the leaf and the entire canopy (WULLSCHLEGER *et al.* 1998). Single leaf measurements can overestimate true whole-plant photosynthesis by as much as 40 % in grapevines and fruit trees (EDSON *et al.* 1995, KATERJI *et al.* 1994, PONI *et al.* 1997). Spatial and temporal variation in gas exchange and complex interactions between the plant and the environment make extrapolations difficult (BUWALDA 1991, BUWALDA *et al.* 1992, INTRIERI *et al.* 1997, LONG *et al.* 1996, SUCCI and MAGNANINI 1994, WÜNSCHE and PALMER 1997). In addition, whole canopies may have higher apparent values for light compensation and light saturation points than single leaves (CORELLI-GRAPPADELLI and MAGNANINI 1993, FRANCESCONI *et al.* 1997).

Whole canopy enclosure methods are well adapted to small experimental plot sizes (STEDUTO *et al.* 2002) and overcome some limitations of single leaf gas exchange by integrating the response of the canopy (BUWALDA *et al.* 1992, DAUDET 1987, GARCIA *et al.* 1990). Good enclosure design minimizes disturbance of the plant's natural environment (GARCIA *et al.* 1990). However, even with a highly transparent cover, an enclosure reduces solar radiation in the chamber as well as gas exchange between the plant and the atmosphere (CORELLI-GRAPPADELLI and MAGNANINI 1993, DAUDET 1987, MANDL *et al.* 1973). This "chamber effect" must be minimized by sufficient rates of air exchange and air mixing within the chamber.

Our goal was to construct a gas exchange system that was unattended, moveable, wind resistant, and, using multiple chambers, capable of simultaneously recording measurements from several mature, trellised, field-grown grapevines. Each chamber enclosed a single vine. An open flow-through system was preferable because of the extended

measurement period ( $> 24$  h) and the difficulty of establishing a perfect seal between plant and atmosphere with a large moveable chamber (BROWN 1988, WHEELER 1992). Leakage of air from a well-mixed open chamber has little if any effect on estimated gas exchange, as long as the flow rate of air entering the chamber is measured accurately (GARCIA *et al.* 1990). The system was autonomous in that it was powered by a self-contained gas generator. This paper describes the design and management of a mobile system used to measure net gas exchange of whole field-grown grape vines (*Vitis vinifera* L. cv. Cabernet Sauvignon) under various deficit irrigation regimes in a semi-arid climate. The system can be applied in different areas where studies on whole canopy physiology are of interest.

### Material and Methods

**Chamber design:** Six open, whole canopy gas exchange chambers were designed, built and tested during 2001 and 2002 for use with mature, field-grown grapevines supported by a multiple-wire trellis. Frequent strong winds (e.g.  $\sim 12.5 \text{ m s}^{-1}$ ) at the experimental site required the chambers to be framed, which also simplified installation and repositioning in the field. Chamber dimensions were determined by the volume of canopy to be enclosed (maximum canopy height about 2 m, total leaf area about  $8 \text{ m}^2$ ), the distance between rows (2.7 m), the distance between vines (1.8 m), and the trellis structures (3 horizontal wires at 0.80 m, 1.20 m, and 1.60 m). The modular design accommodated the trellis system without modification, allowing selection of any vine in the vineyard without disturbing vineyard management operations or the trellis wires (Weinstock *et al.* 1982).

Chambers were designed as standing cylinders (2.1 m diameter x 2.0 m height) topped by an open frustum (1.05 m

high; Fig. 1). An ideal shape for a chamber is spherical to maintain the angle of incidence of the radiation onto the chamber as perpendicular as possible (CORELLI-GRAPADELLI and MAGNANINI 1997), while at the same time ensuring sufficient air mixing. A cylinder topped by a frustum improves air circulation by minimizing sharp angles at the outlet and reducing air incursion into the top of the chamber. The chambers were composed of two halves. Support legs (0.45 m high) raised the floor of the chamber above the drip irrigation lines and were retractable to facilitate chamber installation and leveling. Total chamber volume was approximately  $8 \text{ m}^3$ . Although frame members cast shadows on the canopy, the design was structured to minimize this effect. The ratio between frame area and chamber surface area (excluding floor) was 0.058. A small surface : volume ratio also reduces errors due to water adsorption (KNIGHT 1992), although the chamber cladding had stringent adsorption specifications. Framing members were lightweight aluminum (3.17 mm thick). A cylindrical chamber was attained with 4 horizontal rings of flat aluminum (25.4 mm wide; Fig. 1) attached to the vertical parts. The basal ring was 50 mm wide and supported the chamber floor. Angle aluminum (25.4 mm x 25.4 mm) was used for the vertically oriented structures. To seal the chamber and avoid air leaks, closed-cell, adhesive-backed PVC foam strips (2.54 mm wide, 12.7 mm thick,  $0.192 \text{ g cm}^{-3}$  density) were attached to the vertical aluminum structure of one of the halves along the contact area with the other half. U-shaped aluminum clamps were used to join the halves, compressing the foam strip and sealing the chamber from incursion of outside air. Once installed in the vineyard, the chambers were secured to trellis posts in adjacent rows by 4 ropes. The chamber floor was 5 cm thick polystyrene foam (Styrofoam®; Dow, Midland, MI). A piece of foam was wrapped and tied around the vine trunk to approximate a circular section and eliminate irregularities that might cause

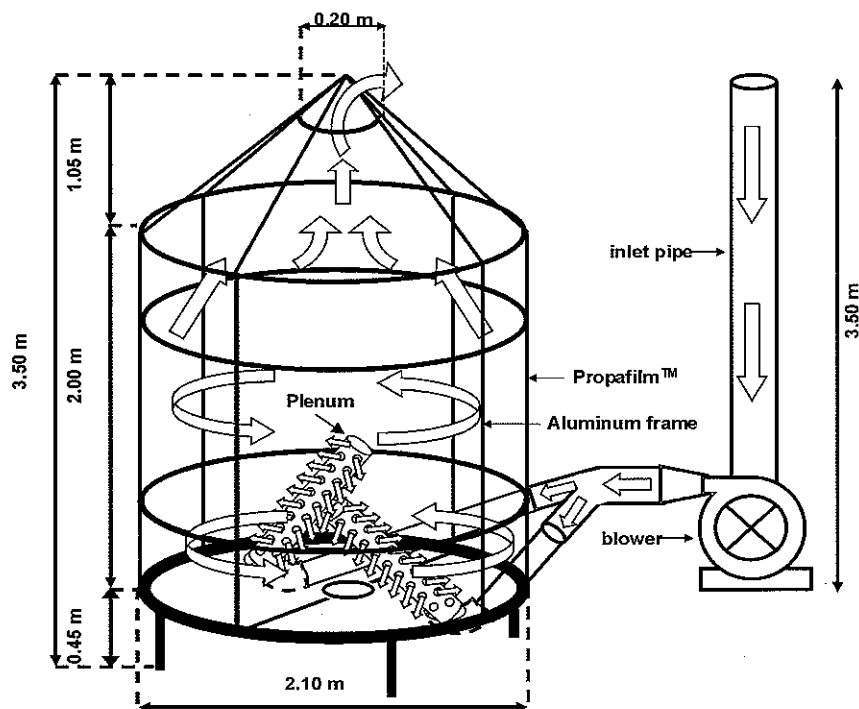


Fig. 1: Schematic diagram of whole-canopy gas exchange chamber used on trellised, field-grown grapevines. Arrows denote air flow.

air leaks at the base of the chamber. A semicircle (0.13 m radius) was cut at the edge of each half floor, so that when the chamber was closed, the flooring sealed the foam around the vine (Fig. 2 A, B).

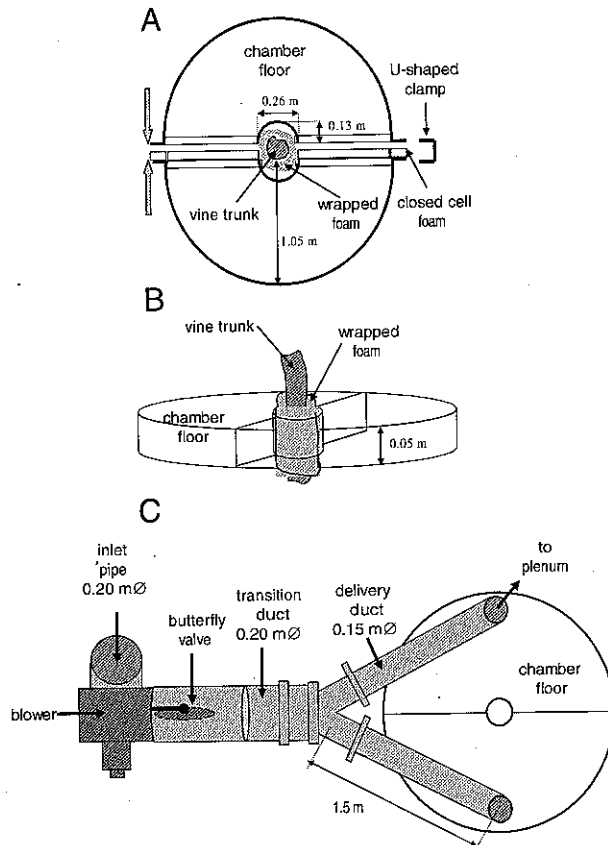


Fig. 2: Schematic diagrams of the chamber floor (not drawn to scale). A: top view; B: side view; C: details of the air conducting system.

The chambers were clad in a biaxially oriented polypropylene (RX 140-Propafilm™-UCB Films Inc, Smyrna, GA), having a nominal thickness of 0.035 mm, thermal transmission of 70 % (2.5  $\mu\text{m}$  -20  $\mu\text{m}$ ), permeability to  $\text{CO}_2$  of  $4 \times 10^{-9} \mu\text{mol m}^{-2} \text{s}^{-1} \text{mm}^{-1}$  (thickness)  $\text{Pa}^{-1}$  (gradient), and water absorption  $< 0.005 \%$  over 24 h (GARCIA *et al.* 1990). Propafilm™ has the highest long-wave transmissivity of suitable, commonly available claddings for gas exchange chambers (Hunt 2003), and is inexpensive. The absorbance of Propafilm™ between 200 nm and 1100 nm was measured with a spectrophotometer (DU® 640, Beckman, Fullerton, CA) at 50 nm intervals. Total radiative absorbance of the polypropylene film was about 0.06 to 0.08 in the visible range (400-700 nm) and about 0.05 to 0.06 in the near infrared (700-1100 nm). The cladding did not significantly modify the spectrum of incident solar radiation. Integrated over 24 h, the maximum reduction in irradiance was 10 % for either cloudy or clear skies. Double sided tape for aluminum and plastic was used to adhere the film to the aluminum frame (9495 LE, 3M, Minneapolis, MN).

Ambient air was delivered to the chamber by a split capacitor blower ( $2.7 \times 10^4 \text{ l min}^{-1}$ ; Dayton No. 7086-0201, Chicago, IL) with round inlet (0.16 m diameter) and rectangular outlet (0.14 m  $\times$  0.18 m). Galvanized sheet metal pipe

was used for drawing ambient air into the blower and directing it to the chamber. Air intake was 3.5 m above the ground to minimize fluctuations in ambient  $\text{CO}_2$ . The blower was connected to a transition duct that converted the rectangular exit to a circular section (0.20 m diameter) that then branched into two smaller (0.15 m diameter) delivery ducts beneath the chamber. A butterfly valve inside the 0.20 m diameter pipe was used to vary manually the flow rate (Fig. 2 C). Air was distributed inside the chamber by two plenums (Fig. 1), one in each half of the chamber, made of 0.15 m diameter, low density (100  $\mu\text{m}$  thick) polyethylene tubes, with 132 uniformly distributed (19 mm diameter) perforations. The plenums were inclined approximately  $35^\circ$ . This inclination was determined after assessing visually the direction of the air streams during a test of the air circulation pattern inside the chamber by igniting smoke candles (Smoke No. 2B 60 second, Superior Signal Company, Spotswood, NJ) at the inlet pipe of the chamber. Smoke tests also indicated where in the chambers the air samples should be taken.

Air temperatures at the inlet and outlet of the chamber were measured by thermocouples (type T, 24 AWG). Inlet thermocouples were located inside the inlet pipe, after the blower and before the plenum. For the outlet air, shielded thermocouples were hung 0.5 m below the top of the frustum of the chamber. Shielded thermocouples also were hung in the canopy at 1.6 m (mean canopy height). Global irradiance was measured by a pyranometer (LI-200SA, LI-COR, Lincoln, NE) and incident photosynthetic photon flux density (PPFD) by a quantum sensor (LI-190S-1, LI-COR, Lincoln, NE), both located outside the chambers.

Air was sampled continuously from 0.75 m below the chamber frustum at a rate of  $15 \text{ l min}^{-1}$  with three, dual-head vacuum pumps (Mod. 400-2901, Barnant Company, Barrington, IL) and was delivered to the infrared gas analyzer (IRGA, Ciras - DC, PP Systems, Haverhill, MA) by bi-layer tubing consisting of polyethylene liner and a shell of ethyl vinyl acetate (6.35 mm I.D., 7.93 mm O.D., Bev-A-Line®, Thermoplastic Processes Inc., Stirling, NY). Fittings were polypropylene (United States Plastic Corporation, Lima, OH).

Ambient  $[\text{CO}_2]$  and  $\text{H}_2\text{O}$  pressure were measured in air drawn continuously by a vacuum pump (UN815, KNF Neuberger INC, Trenton, NJ) from the middle of the vineyard at a height of 3.5 m and at a rate of  $15 \text{ l min}^{-1}$ . All sampled air was under positive pressure from the pumps to the IRGA. Concentrations of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  pressure at the chambers' outlets were measured by the IRGA. The measurement range was from 0 to  $2000 \mu\text{mol mol}^{-1}$  with a precision of  $0.2 \mu\text{mol mol}^{-1}$  at  $300 \mu\text{mol mol}^{-1}$  for  $\text{CO}_2$ . For  $\text{H}_2\text{O}$ , its range was 0 to 75 mb with a precision of 0.02 mb at 10 mb. A gas multiplexer (GHU 161, ADC Bioscientific Ltd., Hoddesdon, England) switched the sample streams among the 6 chambers. All data were recorded by datalogger (Model CR7, Campbell Scientific, Logan, UT). The IRGA was zeroed every 30 min and calibration was checked after each field run using certified gas (359 and 305 ppm of  $\text{CO}_2$ , Air Liquid™, Houston, TX) and a humidity calibrator (PP Systems, Haverhill, MA).

**System operation and testing:** The 6 chambers (Fig. 3) operated simultaneously, powered by a gasoline generator (5 kW; Onan Marquis 5000, Cummings,

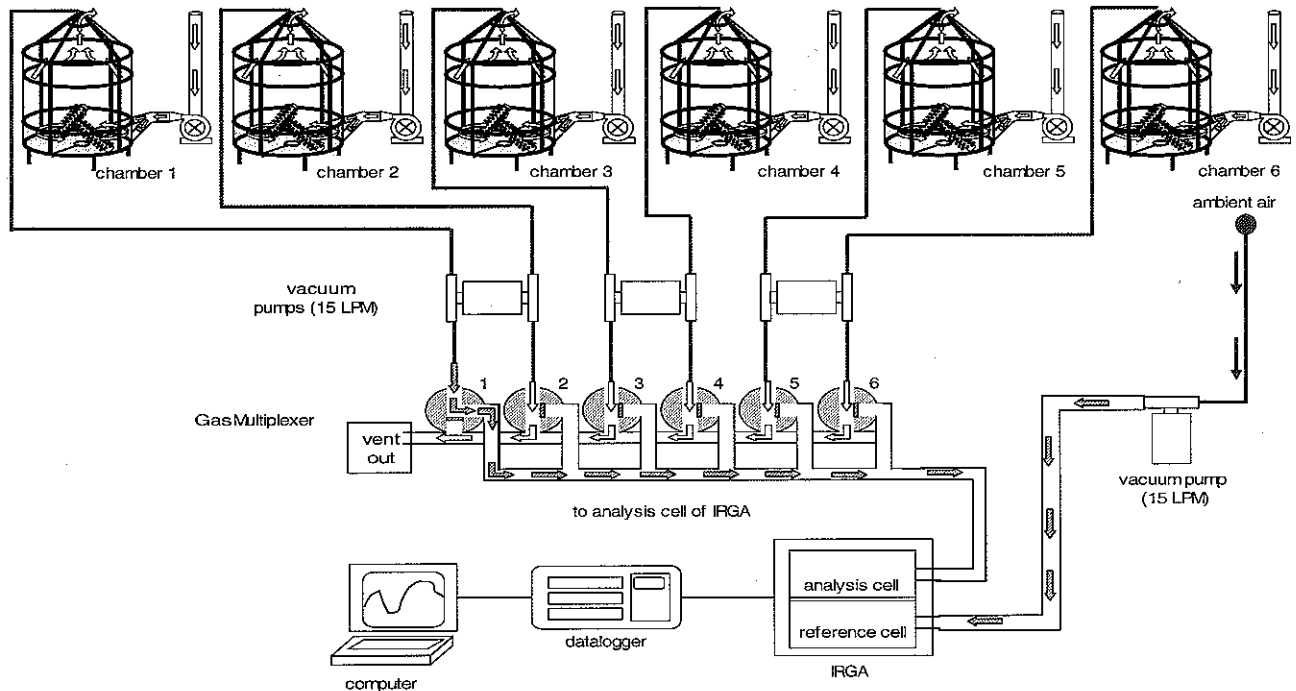


Fig. 3: Schematic diagram of whole-canopy gas exchange system for several, field-grown vines.

IN). A field trailer housed all instrumentation (e.g., IRGA, gas multiplexer, air sampling pumps, and datalogger). Air from one chamber at a time was directed to the IRGA by the gas multiplexer during a 2 min period. Air from the other 5 chambers was by-passed and vented outside. During the final 30 s of the 2 min interval, the datalogger recorded the IRGA output signal every 2.5 s, then computed a 30 s average. Every 2 min, the sample air stream from the next chamber in sequence was directed to the IRGA. Thus, data from each chamber were collected every 12 min. The time taken for the air sampled from the chamber to reach the gas multiplexer (60 m between the chamber and the gas multiplexer) was 7.6 s, and to the IRGA it was 20 s. Any vine within 60 m of the trailer housing the instruments could be measured.

On two days with clear skies (DOY 298, 2001, and DOY 192, 2002) temperatures inside and outside a chamber were measured at different heights above the ground (0.90 m, 1.40 m, 1.90 m, 2.40 m, and 2.90 m) with shielded thermocouples (type T, 24 AWG) mounted to a wooden frame. Temperatures were recorded every 5 s and averaged every 2 min. Irradiance was measured with two pyranometers (LI-200SA, LI-COR Inc, Lincoln, NE) installed inside and outside the chamber on DOY 299 (cloudy) and DOY 300 (clear) of 2001. Data were recorded every 5 s and averaged every 12 min by datalogger. Wind speed at the site was measured at 2 m height by a 3-cup anemometer (12102D, R. M. Young, Traverse City, MI). Both 12 min averages and daily maxima were recorded.

Because net gas exchange in an open system is proportional to the flow rate of air across the canopy it is critical to measure the flow rate accurately. Air flow through the chambers was monitored continuously by differential pressure sensors (Model PX170-07DV, Omega Eng. Inc., Stamford, CT) installed in each chamber and calibrated against the flow as measured by a gas dilution technique (GARCIA *et al.*

1990). Briefly, at the inlet pipe of the chamber before the blower, 98 % pure CO<sub>2</sub> was injected with a highly accurate flowmeter ( $\pm 5$  %, FM-1050 Series, Matheson, Montgomeryville, PA) specifically calibrated for CO<sub>2</sub>. Before and after the injection point, air was sampled at 15 l min<sup>-1</sup>. Post-injection sampling was beyond the blower but ahead of the plenums. This calibration procedure allowed us to calibrate the blower with the vine enclosed in the chamber, which is important because the plant can change a calibration curve performed on an empty chamber (HAM *et al.* 1993). The flow calibration was re-checked in all chambers at the end of every 7-day measurement run. Blower speed (rpm) was measured with a photo-tachometer and stroboscope (Model 4618258, Exttech Instruments, Tampa, FL). With the butterfly valve completely open, flow through the chamber was about 16 m<sup>3</sup> min<sup>-1</sup> (maximum flow), resulting in two chamber volumes being exchanged per minute. With the valve completely closed, flow was about 2.8 m<sup>3</sup> min<sup>-1</sup> (minimum flow). The flow was kept at maximum during the day and at minimum during the night.

Net gas exchange rates were calculated from the differences in [CO<sub>2</sub>] and H<sub>2</sub>O pressure between the air exiting and entering the chamber, adjusted for the rate of air flow across the chamber. The decline in molar [CO<sub>2</sub>] by photosynthesis is very small compared to that of H<sub>2</sub>O addition, so the reduction in [CO<sub>2</sub>] was not considered in transpiration calculations (FIELD *et al.* 1989). To express net gas exchange rate on the basis of canopy leaf area, total leaf area per vine was estimated by a 3 step process: (1) leaf width was regressed against leaf area for a sample of 200 leaves ( $r^2 = 0.96$ ); (2) the widths of all leaves on a sample of shoots ( $n = 8$ ) were measured, and individual leaf areas computed from the relationship established in (1); and (3) leaf area per vine was calculated from the average leaf area per shoot in the sample and the recorded number of shoots per vine.

## Results and Discussion

**Chamber design and operation:** Due to frequent, strong winds at the experimental site, a balloon type chamber was impractical. The frame and the ropes that attached the chambers to the trellis made them stable enough to resist sustained winds over  $13 \text{ m s}^{-1}$  and higher gusts. A framed chamber also allowed us to maintain chamber shape and volume regardless of blower output or wind variation, thereby minimizing temporal variation in the vine boundary layer and reducing the incidence of air pockets, an advantage over balloon-style enclosures. Visual examination of smoke infiltration into the chamber showed thorough mixing in  $< 40 \text{ s}$ . The light weight frame allowed two people to move and secure the chamber from vine to vine in less than 30 min. Flow rates to the chamber were selected according to three criteria: (1) the expected acceptable rise in air temperature in the chamber; (2) the acceptable reduction in  $[\text{CO}_2]$  between inlet and outlet; and (3) the available power for the blowers and instruments.

Expected  $\Delta T_a$  according to flow rate and chamber design can be approximated by (GARCIA *et al.* 1990):

$$\Delta T_a = H \times \left[ \left( \frac{f \times M \times c_p}{A_b} \right) + \left( \frac{A_w \times \rho_a \times c_p}{2 \times r_H \times A_b} \right) \right]$$

where  $H$  is heat absorbed ( $\text{W m}^{-2}$ );  $\Delta T_a$  is the temperature difference between inside and outside of the chamber ( $^{\circ}\text{C}$ );  $f$  is air flow ( $\text{mol s}^{-1}$ );  $M$  is the molecular weight of air ( $29 \text{ g mol}^{-1}$ );  $c_p$  is the specific heat of air ( $1.01 \text{ J g}^{-1} ^{\circ}\text{C}^{-1}$ );  $A_b$  is basal area of chamber ( $\text{m}^2$ );  $A_w$  is wall area of chamber ( $\text{m}^2$ );  $\rho_a$  is the density of air ( $1.183 \times 10^3 \text{ g m}^{-3}$  at  $25 ^{\circ}\text{C}$  and  $100 \text{ kPa}$ ); and  $r_H$  is resistance to heat transfer for wall surfaces under forced convection ( $\text{s m}^{-1}$ ). Heat absorbed ( $H$ ) was calculated following CAMPBELL and NORMAN (1998). A rise in temperature of  $3 ^{\circ}\text{C}$  (Fig. 4) was estimated for two chamber volumes per minute. A reduction in transpiration due to vine water stress would reduce the fraction of  $H$  dissipated by transpiration, consequently increasing the temperature of the chamber parts and the enclosed vine. For criterion (2), a depletion above  $30 \mu\text{mol mol}^{-1} \text{ CO}_2$  between inlet and outlet was avoided, the practical level used in closed systems (LONG and HÄLLGREN 1989). Criteria (1) and (2) are related as higher flow through the chamber (*i.e.* more chamber volumes exchanged per minute) will reduce the rise in temperature throughout the chamber, but at the same time also will reduce  $[\text{CO}_2]$  depletion. The depletion must be large enough to be detected by the IRGA, but not so large that  $[\text{CO}_2]$  is reduced significantly below ambient.

**Chamber microclimate:** On DOY 192, 2002 (Fig. 5), maximum temperatures inside the chamber at the highest and lowest positions were  $47.2 ^{\circ}\text{C}$  (2.9 m) and  $42.5 ^{\circ}\text{C}$  (0.9 m). Outside temperatures at the same positions were  $42.5 ^{\circ}\text{C}$  and  $40 ^{\circ}\text{C}$ , respectively. On DOY 298, 2001, also a day with clear skies (data not shown), maximum air temperatures ( $T_a$ ) inside the chamber were  $19 ^{\circ}\text{C}$  at the highest (2.9 m) thermocouple position and  $15 ^{\circ}\text{C}$  at the lowest position (0.9 m above ground). Outside temperatures at the same heights were  $15 ^{\circ}\text{C}$  and  $13.8 ^{\circ}\text{C}$ , respectively. The maximum  $\Delta T_a$  con-

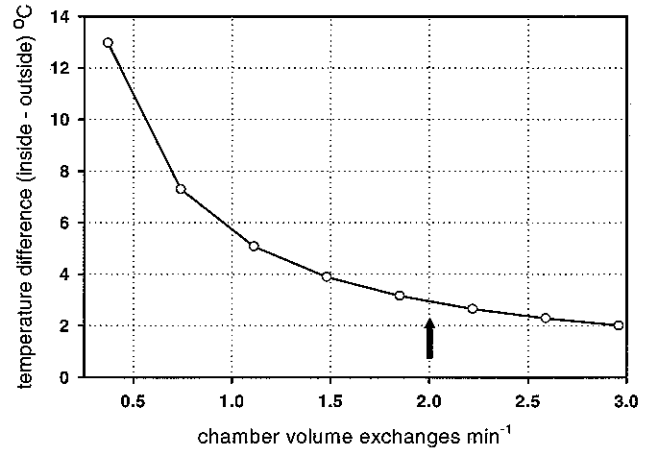


Fig. 4: Estimation of the temperature difference between outside and inside the chambers based on the flow rate through the chamber. Arrow indicates the typical daytime ventilation rate. Calculations for DOY 157, under clear skies and  $35 ^{\circ}\text{C}$  ambient air temperature. Transpiration was assumed to dissipate half of the heat absorbed.

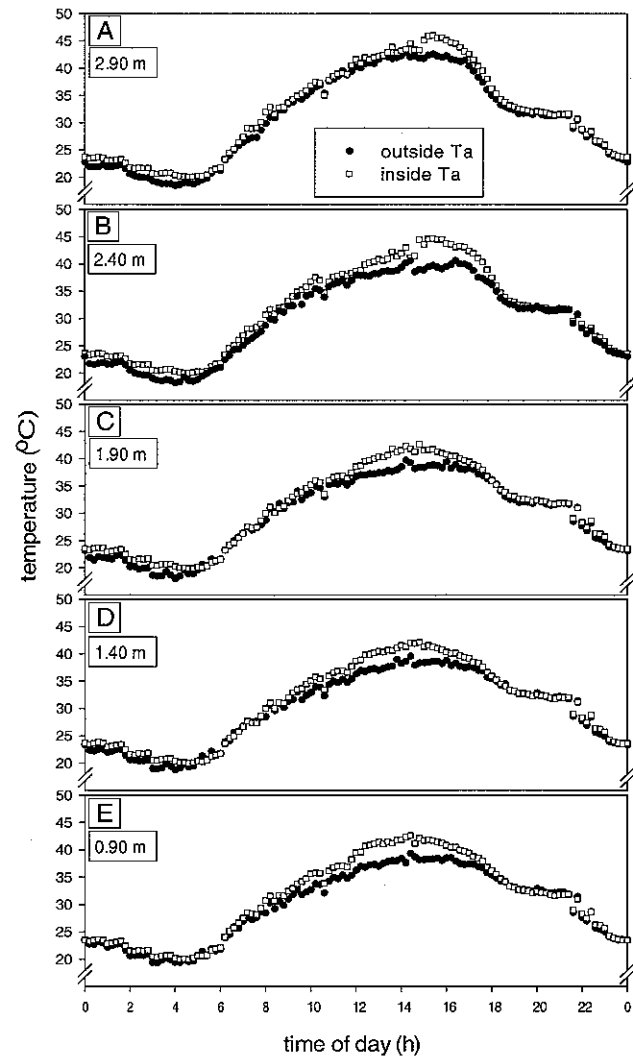


Fig. 5: Diurnal pattern of air temperature inside and outside the chamber at 5 different heights above ground. Data were collected on DOY 192, 2002. Flow through the chamber was  $16 \text{ m}^3 \text{ min}^{-1}$  (about two chamber volumes per minute).

sistently occurred at the two highest measurement positions (2.40 m and 2.90 m above ground) and were under 5 °C, regardless of absolute ambient temperatures. At measurement heights corresponding to the canopy (1.90 m and 1.40 m above ground) and at maximum flow rates (2 chamber volumes min<sup>-1</sup>), air exchange was sufficient to keep  $T_a$  at canopy height within 2.5 °C of that in an un-enclosed vine canopy during a warm day (40 °C) with clear skies.

Higher  $T_a$  inside the chamber modifies gas exchange rates in at least two ways: (1) a direct effect of temperature on photosynthesis and (2) an indirect effect of temperature on vine physiology by its influence on leaf temperature and the vapor pressure deficit between leaf and air ( $VPD_{la}$ ). Temperature effects on photosynthesis in grapevines have been better established at the single leaf level (DOWNTON *et al.* 1987, GAMON and PEARCY 1990 a, WILLIAMS *et al.* 1994, JACOBS *et al.* 1996). At the whole-canopy level, the influence of temperature is not as clear as in single leaves, particularly in this case where the maximum  $\Delta T_a$  at canopy height was 2.5–3.0 °C. In whole canopies, leaves are under different levels of irradiance, water status, and temperature, so the exact chamber effect on whole-canopy photosynthesis is not easy to predict. In single leaf measurements of *Vitis californica*, photosynthesis declined severely in high-light leaves only if  $T_a$  exceeded 45 °C (GAMON and PEARCY 1990 b). At the same high  $T_a$ , shaded leaves did not show the same degree of reduced photosynthesis.

Air temperature influences physiology indirectly via leaf temperature and stomatal behavior by way of  $VPD_{la}$  (FARQUHAR and SHARKEY 1982, EL-SHARKAWY *et al.* 1985, LAWSON *et al.* 2002, SCHULZE 1986). Assuming the water vapor pressure of the air ( $e_a$ ) entering the chamber is ambient, and considering a relative humidity (RH) on a summer day of 0.25, with  $T_a$  of 40 °C, the air VPD will be 5.53 kPa. An increase in  $T_a$  of 3 °C due to the “chamber effect” would increase  $VPD_{la}$  to 6.87 kPa, 1.34 kPa higher than for a non-enclosed vine, if the increase in  $T_a$  is accompanied by the same increase in leaf temperature. Using the Penman-Monteith equation (MONTEITH and UNSWORTH 1990) to estimate canopy transpiration, an increase in  $\Delta T_a$  of 3 °C would result in an approximately 2 % increase in transpiration, which we considered a small environment modification caused by the chamber.

In *Vitis* species an increase in  $VPD_{la}$  tends to decrease stomatal conductance ( $g_s$ ; JARVIS and MORRISON 1981, DÜRING 1987, JACOBS *et al.* 1996). In some single-leaf photosynthesis measurements on *Vitis* species (CHAVES *et al.* 1987, DOWNTON *et al.* 1987) both  $T_a$  and  $VPD_{la}$  varied simultaneously. This, together with the occurrence of stomata in patches on grapevine leaves, could make it difficult to interpret data and scale up from single leaf to whole canopy (SCHULTZ *et al.* 1996). JACOBS *et al.* (1996) used a model that included net photosynthesis ( $A_n$ ) and  $g_s$  to explain that  $VPD_{la}$  may have a larger effect on  $g_s$  than on  $A_n$ . With increasing  $VPD_{la}$ , the difference between ambient  $[CO_2]$  and leaf internal  $[CO_2]$  increases, and under these circumstances net  $CO_2$  assimilation in grapes apparently is less affected than is transpiration (CHAVES *et al.* 1987, WILLIAMS *et al.* 1994). The chamber effect, via an increase in the vine’s boundary layer, results in leaves being less coupled to  $VPD_{la}$ , par-

ticularly if the ventilation rate through the chamber is less than that around an un-chambered vine (JARVIS and McNAUGHTON 1986, WULLSCHLEGER *et al.* 1998).

**Net gas exchange:** During mid-season under clear skies at an air exchange rate of two chamber volumes per minute (16 m<sup>3</sup> min<sup>-1</sup>), the maximum differences in  $[CO_2]$  and  $H_2O$  between air entering and exiting the chamber were around 12  $\mu\text{mol mol}^{-1}$  and 2.5 mb, respectively. Other values reported for open-system chambers are between 4.5 and 40  $\mu\text{mol mol}^{-1}$   $[CO_2]$  (PONI *et al.* 1997, less than 40  $\mu\text{mol mol}^{-1}$ , MILLER *et al.* 1996, between 15 and 35  $\mu\text{mol mol}^{-1}$ , CORELLI-GRAPPADELLI and MAGNANINI 1993, 30  $\mu\text{mol mol}^{-1}$ , WÜNSCHE and PALMER 1997, 4.5  $\mu\text{mol mol}^{-1}$   $[CO_2]$  differential). In this experiment under standard irrigation, 70 % of the calculated vineyard evapotranspiration (ET) was replaced weekly by drip irrigation. Stressed vines received irrigation equivalent to 35 % of ET. Net  $CO_2$  exchange was higher for vines under standard irrigation (maximum rate about 12  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) than under water stress (maximum rate about 6.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Transpiration in both irrigation schemes responded to transient changes in solar radiation (Fig. 6). Transpiration was

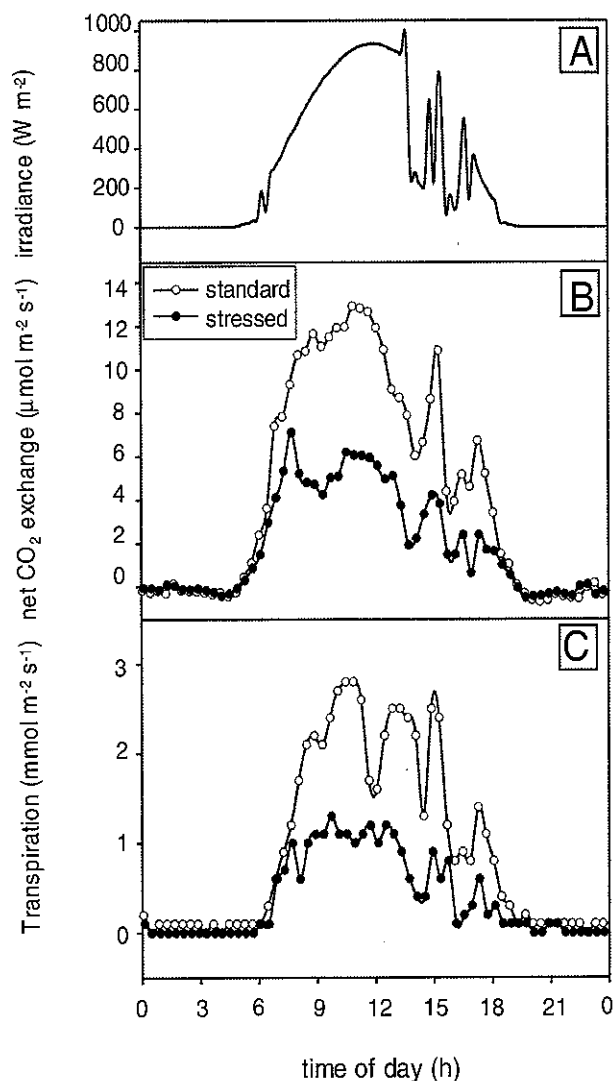


Fig. 6: Diurnal curve of global irradiance (A), net  $CO_2$  exchange rate (B), and transpiration (C) for an exemplary vine under standard irrigation and for a vine under imposed water stress. DOY 218, 2002.

higher in vines under standard irrigation (maximum about  $3 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) than in stressed vines (about  $1 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ). Photosynthetic response to PPFD also differed between standard irrigated vines and stressed vines (Fig. 7). Apparent light response curves were built combining the data from the quantum sensor and net  $\text{CO}_2$  exchange from predawn to noon. The apparent light response curve of a vine under water stress saturated at one-third lower PPFD (about  $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) than did a vine under standard irrigation (about  $1200 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD). At PPFD levels  $> 800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , photosynthesis may have been limited in the water stressed vines by water status rather than by light *per se*. Water use efficiency (WUE), the ratio of net  $\text{CO}_2$  exchange ( $\text{mmol m}^{-2} \text{ s}^{-1}$ ) to transpiration ( $\text{mol m}^{-2} \text{ s}^{-1}$ ) averaged 4.0 for vines under standard irrigation and 6.4 for stressed vines. Other work in grapes, using single-leaf measurements, reported WUE between 1.2 to 3.2 (PONI *et al.* 1994) and between 1 and 8 (SCHULTZ 2000) depending on the leaf position along the shoot, water status, variety, time of day, and time of year. Differences in transpiration between irrigation levels may have caused the temperature of the air exiting the chamber around stressed vines to be 1 or  $2^\circ\text{C}$  higher than the air exiting a chamber around a standard irrigated vine.

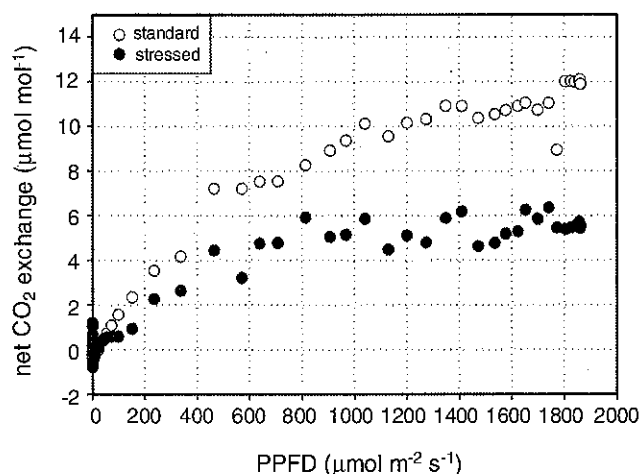


Fig. 7: Apparent light response of photosynthesis for an exemplary vine under standard irrigation and for a vine under imposed water stress. DOY 218, 2002.

### Conclusion

A whole-canopy gas exchange system was designed and used to measure photosynthesis and transpiration simultaneously on several mature field-grown, trellised grapevines. Modifications to light and temperature inside the chamber were minimal, with canopies no warmer than  $2.5^\circ\text{C}$  above ambient and irradiance reduced by less than 10 %. Net  $\text{CO}_2$  and  $\text{H}_2\text{O}$  exchange rates between vines under different levels of imposed water stress were different. Maximum net  $\text{CO}_2$  exchange rates were about  $12 \mu\text{mol m}^{-2} \text{ s}^{-1}$  for standard irrigated and about  $6.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$  for water stressed vines. Maximum transpiration rates were under  $3 \text{ mmol m}^{-2} \text{ s}^{-1}$  for vines irrigated by the industry standard method, and about  $1 \text{ mmol m}^{-2} \text{ s}^{-1}$  for vines irrigated at 50 %

of the standard amount. Differences in photosynthetic light responses were detected between irrigation levels. Because the chambers were portable and lightweight, the whole system (chambers and instrumentation) was quickly and easily assembled in the vineyard in under 20 man-hours, allowing for measurements during short periods. Moving a chamber from vine to vine along the same row required 0.5 man-hours. No modification to the original canopy of the grapevine or the trellis system was required (*i.e.*, pruning, shoot removal, or cutting wires). The system can control at least 6 chambers depending on available power and labor. The cylindrical design of the chamber promoted air circulation and rapid mixing of the air inside the chamber, without formation of air pockets. High rates of air pumping ( $15 \text{ l min}^{-1}$ ) made it possible to choose any vine up to 60 m from the instrument trailer, thereby avoiding edge effects. Because the aluminum frame improved chamber resistance to wind, the chambers could be deployed during more days of the year, thus increasing the frequency of measurements and allowing for sufficient replication. The system designed here proved to be a suitable research tool for measuring whole-plant gas exchange and for understanding the effects of different environmental conditions and viticultural practices on whole vine physiology.

### References

- BROWN, M. S.; 1988: Design considerations for a system to measure net carbon dioxide exchange in intact plants. *Int. Agrophys.* **4**, 69-81.
- BUGBEE, B.; 1992: Steady-state canopy gas exchange: system design and operation. *HortScience* **27**, 770-776.
- BUWALDA, J. G.; 1991: A mathematical model of carbon acquisition and utilization by kiwifruit. *Ecol. Modell.* **57**, 43-64.
- BUWALDA, J. G.; GREEN, T. G. A.; MEEKINGS, J. S.; CONEYBEAR, D. J.; 1992: Measurement of canopy gas exchange of kiwifruit vines using a suite of whole canopy cuvettes. *Environ. Exp. Bot.* **32**, 439-448.
- CAMPBELL, G. S.; NORMAN, J. M.; 1998: Radiation fluxes in natural environments. In: *An Introduction to Environmental Biophysics*, 2nd ed., 167-184. Springer-Verlag New York, Inc.
- CHAVES, M. M.; HARLEY, P. C.; TENHUNEN, J. D.; LANGE, O. L.; 1987: Gas exchange studies in two Portuguese grapevine cultivars. *Physiol. Plant.* **70**, 639-647.
- CORELLI-GRAPADELLI, L.; MAGNANINI, E.; 1997: Whole tree gas exchanges: Can we do it cheaper? *Acta Hort.* **451**, 279-285.
- CORELLI-GRAPADELLI, L.; MAGNANINI, E.; 1993: A whole tree system for gas exchange studies. *HortScience* **28**, 41-45.
- DAUDET, F. A.; 1987: Un système simple pour la mesure *in situ* des échanges gazeux de couverts végétaux de quelques mètres carrés de surface foliaire. *Agronomie* **7**, 133-139.
- DE PURY, D. G. G.; FARQUHAR, G. D.; 1997: Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell Environ.* **20**, 537-557.
- DOWNTON, W. J. S.; GRANT, W. J. R.; LOVEYS, B. R.; 1987: Diurnal changes in the photosynthesis of field grown grape vines. *New Phytol.* **105**, 71-80.
- DÜRING, H.; 1987: Stomatal response to alterations of soil and air humidity in grapevines. *Vitis* **26**, 9-18.
- EDSON, C. E.; HOWELL, G. S.; FLORE, J. A.; 1995: Influence of crop load on photosynthesis and dry matter partitioning of Seyval grapevines II. Seasonal changes in single leaf and whole vine photosynthesis. *Am. J. Enol. Vitic.* **46**, 469-477.
- EL-SHARKAWY, M. A.; COCK, J. H.; DEL PILAR, A.; 1985: Stomatal response to air humidity and its relation to stomatal density in a wide range of warm climate species. *Photosynth. Res.* **7**, 137-149.
- FARQUHAR, G. D.; SHARKEY, T.; 1982: Stomatal conductance and photosynthesis. *Ann. Rev. Plant Physiol.* **33**, 317-345.

- FIELD, C. B.; BALL, J. T.; BERRY, J. A.; 1989: Photosynthesis: Principles and field techniques, 209-253. In: R. W. PEARCY, J. EHLERINGER, H. A. MOONEY, P. W. RUNDEL (Eds): *Plant Physiological Ecology. Field Methods and Instrumentation*. Chapman and Hall Ltd., New York.
- FRANCESCONI, A. H. D.; LAKSO, A. N.; DENNINGS, S. S.; 1997: Light and temperature effects on whole-canopy net carbon dioxide exchange rates of apple trees. *Acta Hort.* **451**, 287-293.
- GAMON, J. A.; PEARCY, R. W.; 1989: Leaf movement, stress avoidance and photosynthesis in *Vitis californica*. *Oecologia* **79**, 475-481.
- GAMON, J. A.; PEARCY, R. W.; 1990 a: Photoinhibition in *Vitis californica*. The role of temperature during high-light treatment. *Plant Physiol.* **92**, 487-494.
- GAMON, J. A.; PEARCY, R. W.; 1990 b: Photoinhibition in *Vitis californica*: Interactive effects of sunlight, temperature and water status. *Plant Cell Environ.* **13**, 267-275.
- GARCIA, R.; NORMAN, J. M.; McDERMITT, D. K.; 1990: Measurements of canopy gas exchange using an open chamber system. *Remote Sensing Rev.* **5**, 141-162.
- GIAGLARAS, P.; BAILLE, M.; BAILLE, A.; 1995: Net photosynthesis response to light and air CO<sub>2</sub> concentration of *Begonia x hiemalis*: Whole plant measurement and modelling. *Sci. Hortic.* **63**, 83-100.
- HAM, J. M.; OWENSBY, C. E.; COYNE, P. I.; 1993: Technique for measuring air flow carbon dioxide flux in large, open-top chambers. *J. Environ. Qual.* **22**, 759-766.
- HUNT, S.; 2003: Measurements of photosynthesis and respiration in plants. *Physiol. Plant.* **117**, 314-325.
- HUNTER, J. J.; VISSER, J. H.; 1989: The effect of partial defoliation, leaf position and developmental stage of the vine on leaf chlorophyll concentration in relation to the photosynthetic activity and light intensity in the canopy of *Vitis vinifera* L. cv. Cabernet Sauvignon. *S. Afr. J. Enol. Vitic.* **10**, 67-73.
- IACONO, F.; SOMMER, K. J.; 1996: Photoinhibition of photosynthesis in *Vitis vinifera* under field conditions: Effects of light and leaf position. *Aust. J. Enol. Vitic.* **2**, 10-20.
- INTRIERI, C.; PONI, S.; REBUCCI, B.; MAGNANINI, E.; 1997: Effects of canopy manipulations on whole-vine photosynthesis: Results from pot and field experiments. *Vitis* **36**, 167-173.
- JACOBS, C. M. J.; VAN DEN HURK, B. J. J. M.; DE BRUIN, H. A. R.; 1996: Stomatal behaviour and photosynthetic rate of unstressed grapevines in semi-arid conditions. *Agric. For. Meteorol.* **80**, 111-134.
- JARVIS, P. G.; McNAUGHTON, K. G.; 1986: Stomatal control of transpiration: Scaling up from leaf to region. *Adv. Ecol. Res.* **15**, 1-49.
- JARVIS, P. G.; MORRISON, J. I. L.; 1981: The control of transpiration and photosynthesis by the stomata. In: P. G. JARVIS (Ed.): *Stomatal Physiology*, 247-249.
- KATERJI, N.; DAUDET, F. A.; CARBONNEAU, A.; OLLAT, N.; 1994: Etude à l'échelle de la plante entière du fonctionnement hydrique et photosynthétique de la vigne: Comparaison des systèmes de conduite traditionnel et en Lyre. *Vitis* **33**, 197-203.
- KNIGHT, S. L.; 1992: Constructing specialized plant growth chambers for gas exchange research: Considerations and concerns. *HortScience* **27**, 767-769.
- KRIEDEMANN, P. E.; KIEWER, W. M.; HARRIS, J. M.; 1970: Leaf age and photosynthesis in *Vitis vinifera* L. *Vitis* **9**, 97-104.
- LAWSON, T.; OXBOROUGH, K.; MORISON, J. I. L.; BAKER, N. R.; 2002: Responses of photosynthetic electron transport in stomatal guard cells and mesophyll cells in intact leaves to light, CO<sub>2</sub>, and humidity. *Plant Physiol.* **128**, 52-62.
- LONG, S. P.; FARAGE, P. K.; GARCIA, R. L.; 1996: Measurement of leaf and canopy photosynthetic CO<sub>2</sub> exchange in the field. *J. Exp. Bot.* **47**, 1629-1642.
- LONG, S. P.; HALLGREN, J. E.; 1989: Measurement of CO<sub>2</sub> assimilation by plants in the field and the laboratory, 62-94. In: J. COOMBS, D. O. HALL, S. P. LONG, J. M. SCURLOCK (Eds): *Techniques in Bioproductivity and Photosynthesis*. Pergamon Press, Oxford, U.K.
- MANDL, R. H.; WEINSTEIN, L. H.; McCUNE, D. C.; KEVENY, M.; 1973: A cylindrical, open-top chamber for the exposure of plants to air pollutants in the field. *J. Environ. Qual.* **2**, 371-376.
- MONTETH, J. L.; UNSWORTH, M. H.; 1990: *Principles of Environmental Physics*, 2nd ed., Edward Arnold Pub, London, U.K.
- MILLER, D. P.; HOWELL, G. S.; FLORE, J. A.; 1996: A whole plant open gas exchange system for measuring net photosynthesis of potted woody plants. *HortScience* **31**, 944-946.
- NAOR, A.; GAL, Y.; BRAVDO, B.; 1997: Crop load affects assimilation rate, stomatal conductance, stem water potential and water relations of field grown Sauvignon blanc grapevines. *J. Exp. Bot.* **48**, 1675-1680.
- PETRIE, P. R.; TROUGHT, M. C. T.; HOWELL, G. S.; 2000: Influence of leaf aging, leaf area and crop load on photosynthesis, stomatal conductance and senescence of grapevine (*Vitis vinifera* L. cv. Pinot noir). *Vitis* **39**, 31-36.
- PONI, S.; INTRIERI, C.; SILVESTRONI, O.; 1994: Interactions of leaf age, fruiting, and exogenous cytokinins in Sangiovese grapevines under non-irrigated conditions. I. Gas exchange. *Am. J. Enol. Vitic.* **45**, 71-78.
- PONI, S.; MAGNANINI, E.; REBUCCI, B.; 1997: An automated chamber system for measurements of whole vine gas exchange. *HortScience* **32**, 64-67.
- SCHULTZ, H. R.; 1993: Photosynthesis of sun and shade leaves of field grown grapevines (*Vitis vinifera* L.) in relation to leaf age. Suitability for the plastochron concept for the expression of physiological age. *Vitis* **32**, 197-205.
- SCHULTZ, H. R.; 2000: Physiological mechanisms of water use efficiency in grapevines under drought conditions. *Acta Hort.* **526**, 115-136.
- SCHULTZ, H. R.; KIEFFER, W.; GRUPPE, W.; 1996: Photosynthesis duration, carboxylation and stomatal limitation of sun and shade leaves of different ages in field-grown grapevine (*Vitis vinifera* L.). *Vitis* **35**, 169-176.
- SCHULZE, E. D.; 1986: Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Ann. Rev. Plant Physiol.* **37**, 247-274.
- SILVESTRONI, O.; PONI, S.; INTRIERI, C.; FONTANA, M.; 1993: Effects of light regimes on chlorophyll concentration and gas-exchange in *Vitis vinifera* L. Proc. Of the 3<sup>rd</sup> Int. Symp. on Viticulture and Enology in Cool Climates. Geisenheim/Mainz 8-12 June 1992. *Die Weinwissenschaft. Vitic. Enol. Sci.* **3** (6), 96-100.
- STEDUTO, P.; ÇETINKÖKÜ, Ö.; ALBRIZIO, R.; KANBER, R.; 2002: Automated closed-system canopy-chamber for continuous field-crop monitoring of CO<sub>2</sub> and H<sub>2</sub>O fluxes. *Agric. For. Meteorol.* **111**, 171-186.
- SUCCI, F.; MAGNANINI, E.; 1994: Daily measurement of CO<sub>2</sub> assimilation rate on kiwifruit vine. *New Zealand J. Crop Hortic. Sci.* **22**, 17-21.
- WEINSTOCK, L.; KENDER, W. J.; MUSSELMAN, R. C.; 1982: Microclimate within open-top air pollution chambers and its relation to grapevine physiology. *J. Am. Soc. Hortic. Sci.* **107**, 923-929.
- WHEELER, R. M.; 1992: Gas-exchange measurements using a large, closed plant growth chamber. *HortScience* **27**, 777-780.
- WILLIAMS, L. E.; DOKOOZLIAN, N. K.; WAMPLE, R.; 1994: *Grape. Handbook Environ. Physiol. Fruit Crop* **2**, 85-133.
- WULLSCHLEGER, S. D.; MEINZER, F. C.; VERTESSY, R. A.; 1998: A review of whole-plant water use studies in trees. *Tree Physiol.* **18**, 499-512.
- WÜNSCHE, J. N.; PALMER, J. W.; 1997: Portable through-flow cuvette system for measuring whole canopy gas exchange of apples trees in the field. *HortScience* **32**, 653-658.
- ZUFFEREY, V.; MURISIER, F.; SCHULTZ, H. R.; 2000: A model analysis of the photosynthetic response of *Vitis vinifera* L. cvs Riesling and Chasselas leaves in the field: I. Interaction of age, light and temperature. *Vitis* **39**, 19-26.

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